

# Beech provenance trial in Sweden

– growth and timber quality evaluation



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Swedish University of Agricultural Sciences, SLU  
Southern Swedish Forest Research Centre  
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# Beech provenance trial in Sweden – growth and timber quality evaluation

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## Abstract

Provenance trials allow to test tree growth differences and meet current requirements for timber quality in a particular experimental site. The aim of this manuscript was to distinguish the differences in growth and timber quality features between European beech (*Fagus sylvatica* L.) provenances at its natural northern European margin – in southern Sweden. Data was obtained from a provenance experiment established in 1995 in Rånna to evaluate the growth and timber quality features of 36 European beech provenances. Statistical analysis was conducted using generalized and linear mixed models, and a *post-hoc* Tuckey's test to check provenance differences on quantitative (diameter at breast height, tree basal area increment, height increment, total height) and qualitative features (crookedness, classification of stem morphology, spike knots above 0.5 meters and below 0.5 meters).

Results show, that the German provenance number 37 (Deister, Lower Saxony) reached the best growth outputs in following variables: diameter at breast height 2020, basal area increment, height increment and total height. German provenance number 39 (Seelzerthurn, Lower Saxony) shows the absolute best performance within classification of stem morphology and within spike knots below 0.5 meters abundance. Romanian Provenance number 150 (Sovata (25)) accomplished the best results within crookedness and spike knots above 0.5 meters abundance. German provenance number 51 (Eitorf 1502/262a – North-Rhine-Whestfalia) was evaluated worst in the following tree characteristics: crookedness, classification of stem morphology and spike knots below 0.5 meters abundance. Swedish and Danish beech provenances showed stable growth without any relevantly negative timber quality features, although they did not differ significantly from other provenances in their growth.

The results demonstrate that the genetic background of studied provenances has an important role in building stand development for numerous timber quality features. New provenance experiments establishment may better understand different provenances responses to the climate change as well as to determine the best provenance for high quality timber on the Swedish market.

**Keywords:** Beech, climate change, growth, provenance, Sweden, timber quality

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## Abbreviations

DBH	Diameter at breast height. Measured by caliper at the height of 130 cm above the ground
HI	Height increment
BAI	Basal area increment
SE	Sweden
DE	Germany
DK	Denmark
HU	Hungary
SK	Slovakia
SI	Slovenia
UA	Ukraine
FR	France
RO	Romania
Long	Longitude
Lat	Latitude
Alt	Altitude
a. s. l.	above sea level



# 1. Introduction

## 1.1. European beech forests and climate change

The threat of predicted increasing temperature and higher occurrence of extreme events, that had been prognosticated by scientists (Mátyás *et al.* 2010), might negatively influence tree species resilience and composition in Europe. It is expected, that some tree species will not be able to adapt to ongoing climate change due to highly fragmented landscapes (Jump & Penuelas 2005) and low migration rate (Davis *et al.* 2005; Mátyás 2005).

Global warming might change set of environmental conditions in the natural range of European beech which could cause decline in its natural niche (Bellard *et al.* 2012). Eilmann *et al.* (2014) argue that climate change does not only cause a reduction of productivity of beech stands, but also elevate mortality rates in certain areas. Kramer *et al.* (2010) expect expansion of beech towards northern edge and decline in southern edge distribution. A tool for climate adaptation is a selective transfer of southern range margins provenances, which are heat- and drought-tolerant and use them in northern altitudes (Huber *et al.* 2014). For example, it is expected that drought in the Mediterranean region will cause changes in abundance and distribution of tree species typical for this region, such as cork oak (*Quercus suber*) and Aleppo pine (*Pinus halepensis*) (Ruiz-Labourdette *et al.* 2013). Further studies demonstrate higher assimilation rates of southern European beech provenances, therefore these provenances show higher photosynthesis rates and bigger mean annual increment (Robson *et al.* 2012). Populations from the southern range margin are expected to testify higher water-stress tolerance and faster growth rates (Wang *et al.* 2021).

Severe damages to the forest ecosystem, caused by biotic (pests and diseases) and abiotic (drought, frost, storms or fires) factors influence the physiology, stand development, inter- and intra- specific competition or spring phenology (Badeau & Bréda 2008). Forest management adaptation to climate change can be particularly developed by foresters, who can decide to plant mixtures, which have positive

effects on biodiversity; choose optimal stocking density; doing proper interventions such as thinnings or to give a priority to manage forest for other than timber purposes. Attention should be paid to use proper planting material, which will meet current requirements appropriate to the forthcoming changes on the respective sites (Mátyás 2016; Kramer & Mátyás 2016). Proper quality forest reproductive material should meet the requirement of being well adapted to habitat conditions prevailing in sites to be restored (Bogunovic *et al.* 2020).

The reason to test different provenances of studied species is clear – rapid environmental changes could cause that original provenances might no more find their ecological optimum in amended conditions. Experimental trials, known as common garden experiments, should clarify, which provenance will respond the best towards sustainable forestry in affected environments. Cultivated selected provenances of the studied species would response to the site of provenance test; the provenances are adapted to the original seed source area and therefore should express differences in their growth in the experimental site (Petkova 2020). It is also desirable to develop rapid, inexpensive early testing procedures in order to determinate drought tolerant clones, provenances or families to be used in future climates (Dvorak 2012).

In Sweden, natural regeneration is widely used in forestry only for pine and beech (Agestam *et al.* 2006). If the proportion of beech increases, it would also be possible to abandon intensive clear-cut system and promote a more environmentally friendly approach to forest management, based on continuous cover forestry, or shelterwood system including natural regeneration, in accordance with Sustainable development goals number 15 “Life on land” and number 13 “Climate action” (United Nations 2021).

The history of beech forests in Sweden is dated back to the Middle Ages, when beech forests covered prevalent areas of Southern Sweden (Brunet 1995). 19<sup>th</sup> century meant a swift change in Swedish forest landscape: wood pastures were transformed into the expansion of dense conifer forests for timber purposes, reducing the broadleaves surface (Brunet *et al.* 2012). The percentage of beech stands in Sweden has fallen even further to the present (Brunet *et al.* 2012), where the percentage of European beech standing stock approaches 2.5 % (Corry & Nilson 2018). There is enormous potential to increase the beech production and compete with spruce timber on the market, which is now questioned in many European countries due to bark beetle outbreak.

Knoke *et al.* (2006) highlighted the main qualitative characteristics of beech timber, which reflect the final price of the timber on the market:

- The red heartwood: it is recommended to shorten the final felling age in order to minimize the formation of the heartwood
- Signs of overgrown old branches
- Signs of old felling damage
- Knobs/ Spike knots: indicators of former presence of branch
- The stem curvature (stem crookedness): deviation from vertical axis of the trunk
- The spiral grain: a helical course of timber fibres around the stem centre
- The growth stresses
- The roughness of bark: smooth/harsh
- Signs of “t-cancer” at the bark

As for quantitative characteristics, it usually applies that larger log diameter is awarded higher price per cubic meter.

The demand for beech forests in Sweden is not only requested for the purpose of high-quality timber, however, forest reserves (irrespective of provenances, but preferably of local beech) are needed to be enlarged to maintain forest biodiversity in Sweden – the core are nemoral, broadleaved forests with native species: *Fagus sylvatica* L., *Quercus robur* L., *Tilia cordata* Mill., *Acer platanoides* L., and *Fraxinus excelsior* L. (Andersson & Angelstam 2001). The remnants of old beech forests in Sweden have usually protective character and usually belong to some National Parks or forest reserves. These forests are the habitat for rare saproxylic species, which are dependent on slowly decomposing wood (Brunet *et al.* 2012).

## 1.2. European beech – the studied species

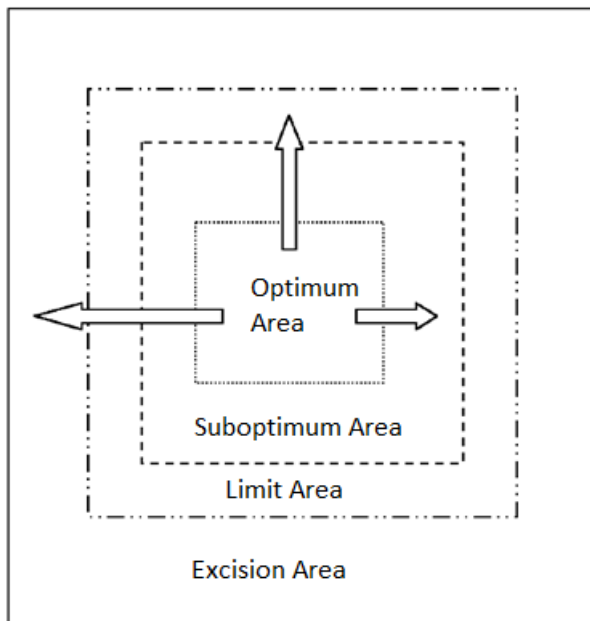
In the past, beech used to be the most important tree species in the hills and foothill areas throughout Central Europe. Its hard and well-workable wood was an important raw material used for the production of many supplies and aids, including charcoal (Barna *et al.* 2011). Its timber can be used for furniture, flooring and engineering purposes (Savill 2013). Beech is generally considered as a species with lower migration variability (Memišević *et al.* 2019), however, according to the poster by Memišević *et al.* 2019, the feature of beech is outstanding by its significant intra-population and inter-population variability. Recent research by Petřík *et al.* (2020) documents, that European beech provenances have shown high

ratio of both adaptation and acclimation after transfer to new environmental conditions. Beech can reach the height of 35 – 40 m and diameter at breast height of 150 cm. The species performs high annual increment up to late ages. Beech usually lives up to 250 years in native forests (Wuhlich 1984).

Beech is regarded as a dominant forest tree species of high economic as well as ecological relevance with a wide distribution range linking Scandinavia and the Mediterranean part of Europe (Sulkowska *et al.* 2011). Climate change predictions presuppose beech to lose habitats in the southern and south-eastern edge of current distribution (Stojnic *et al.* 2013). They report that strong selective pressures in last decades force Southern European margin of common beech (Jump *et al.* 2006; Piovesan *et al.* 2008; Varsamis *et al.* 2018). Phenological cycles of plants are changing; spring leaf phenology occurs earlier, autumn leaf phenology shows delay; which potentially result in a prolonged growing season and thus increasing forest net ecosystem productivity (Homero *et al.* 2019).

Scientists warn against denying negative effects of rapid climate change on European beech forest ecosystems, and recommend to use proper planting stock, which matches the local morphological and future climate conditions (Horváth *et al.* 2016). This is currently followed by European countries. Czech Republic has implemented stringent restrictions on the transfer of planting material between different natural forest areas/ provenances/ altitudes (Flora 2018). This step is to prevent the formation of unstable forests, which might not reach expected final felling age due to biotic and abiotic stressors. In Germany, forest owners are provided by recommendation of usage of different provenances of reproductive material in different regions, although the local provenance is recommended (Bayerisches Amt für Waldgenetik, 2021).

Czajkowski *et al.* (2006a) suggested two possible options as a chance to mitigate negative effects of climate change by silviculture: first, to plant drought-adapted provenances, and second, to select naturally regenerated, local beech populations or provenances. They divided living conditions of a general species according to the degree of optimality / suitability of the species for local living conditions (Figure 1). The areas were set aside so that each additional one connects to the outer boundary of the previously inner one site. The internal (core) site “Optimum area” is surrounded by “Sub-optimum area”, then by “Limit/Border area” and by “Excision area” on the very edge. We can interlink this figure with the Figure of distribution of beech. Scandinavia and Mediterranean nowadays belongs to the “Limit/Border area” of beech distribution. However, as climate is changing, Southern Sweden might shift from the status of Limit/Border area to the status of Sub-optimum area of beech.



*Figure 1: Optimal living conditions. Original figure by Czajkowski, T et al, 2006c modified by translation.*

## 2. Objectives of the thesis

The main objective of this thesis is to evaluate which European beech (*Fagus sylvatica* L.) provenance is better adapted to Swedish conditions to increase growth and timber quality. We proposed to assess tree growth characteristic and timber quality between beech provenances from different European origins established in Southern Sweden.

The specific objectives are:

- (1) To evaluate growth differences (tree basal area increment and height increment) among European beech provenances in comparison to the last inventory in 2008
- (2) To compare timber quality between provenances, especially to evaluate spike knots abundance, crookedness and tendency of tree to fork

The following hypotheses were tested:

- (1) The growth rate of south-eastern European beech provenances should be higher, since these provenances are adapted to harsher climate conditions, especially affected by higher altitude, and should therefore be well adapted to lower mean annual temperatures in the Nordic latitudes
- (2) Swedish and Danish beech provenances should express better growth, since they are naturally adapted to Nordic latitudes

## 3. Material and Methods

### 3.1. Experimental design

The data was collected in March 2020, in the beech provenance experiment S21F9571256 located in Rånna, approximately 10 km north of the city of Skövde, Sweden. The exact coordinates are 58.4511892N, 13.8265236E, sited at 85 m a.s.l. The experiment contains 36 beech provenances, with European origin, including a wide range of varieties with their original features. This can be observed by their original latitude, longitude and altitude: the range includes origins from Sweden in the north to Slovenia in the south; from Germany in the west to Romania in the east (Figure 2). As well as altitudes, ranging from near to a bottom of a sea level (Germany, 25 m), up to mountain provenances originating from 1100 m a.s.l. in Slovenia, create unique vertical range, from which plasticity, diversity, adaptability and response to environmental climatic condition derive. Their detailed description is stated in Table 1 and Table 2.

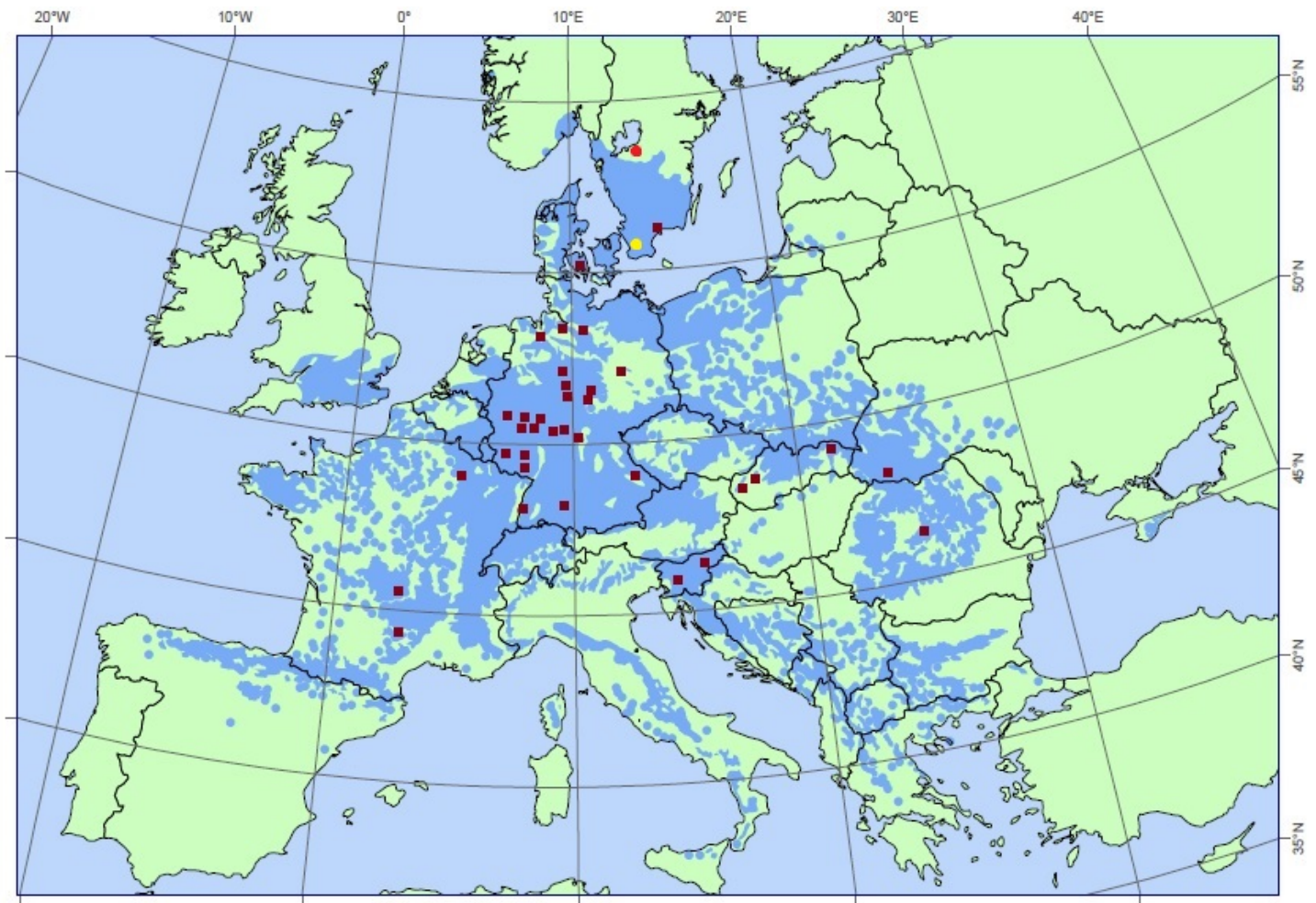


Figure 2: The current European beech distribution in Europe (source: EUFORGEN 2021), study site location and European beech provenances. The red dot indicates position of Rånna trail site. The yellow dot indicates the position of similar trail, established in 1998 in Trolleholm. Brown-purple squares indicate locations of the 36 provenances of beech evaluated in the experiment. Note: Provenances Bidingen Abteilung 762 and Bidingen Abteilung 763 are overlapping on the map, therefore only one square is visible for both of them: their coordinates are after rounding the same: 50.28 N, 9.12 E.

The provenance trail in Rånna was established in 1995 on former agricultural land, using two-year old bare-root seedlings. Planting stock was previously cultivated at the Institute for Forest Genetics and Forest Breeding in Grosshandorf, Germany. The provenance experiment was designed with randomized design and consist of three blocks, where each of them is compiled by 36 individual provenance plots. Each plot is described by a provenance number and plot number. Each plot had 50 individual seedlings with spacing 2 x 1 m at the year of establishment. Each plot has square shape, where the distance between square corners is 10 m. Each individual tree has own position characterized by block number, plot number, provenance number, row number and plant number. The outer edge of the trail is delimited by buffer trees so as to exclude possible edge effect (edge trees are



characterized by different growth patterns caused by higher amount of available light). The trail was established on a fertile soil along a north slope (Skogforsk 2009). The stand is characterized by mean annual precipitation of 678 mm (SHMI 2021). The trend of increasing mean annual temperature for the Skövde climate station is shown in Figure 3.

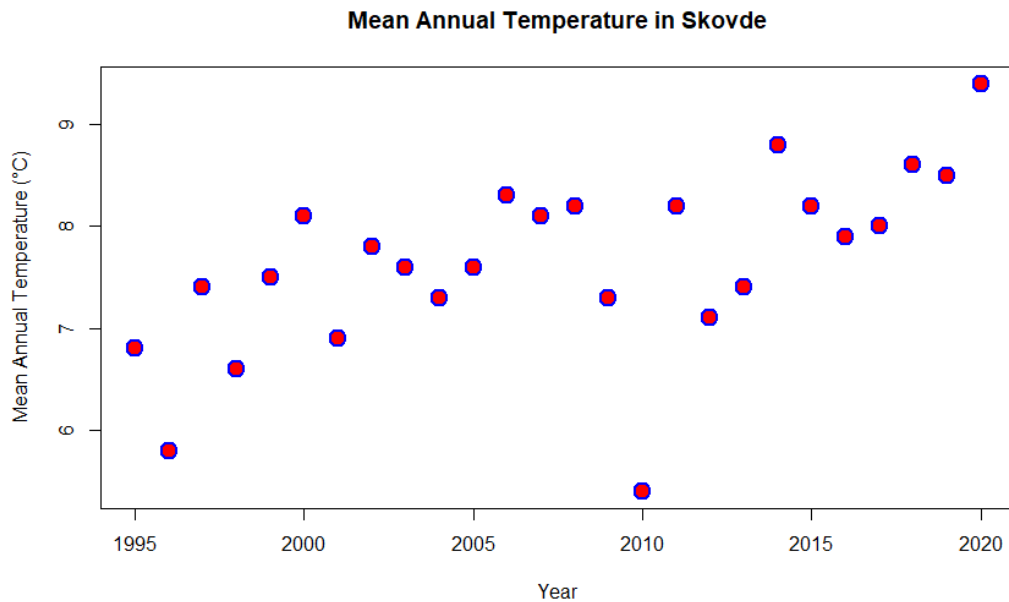


Figure 3: Mean Annual Temperature in the study site. Source: own elaboration from SHMI climate data.

While the mean annual temperature in 1995, when the provenance trial was established, was only 6,8 °C; after twenty-five years, it reached 9,4 °C. This is 2,6 °C increment for 25 years. Although it is not possible to state that the temperature would increase every following year, it is still possible to see the increasing pattern (except one colder year 2010). The data used to create Figure 3 are available online (Kapsi.fi, 2021).

The design of the experiment is depicted in Figure 4.

93	67	161	26	39	36			
18	137	94	51	38	11			
138	43	77	135	144	90			
14	69	88	99	129	87			
80	28	104	37	73	44			
70	92	130	150	66	40	88		
40	37	138	150	161	93	36	73	
38	130	26	129	44	70	137	77	11
92	80	51	94	90	28	99	66	39
43	18	69	144	104	14	67	87	
43	104	161	26	40	38	135		
130	44	36	67	73	11	39		
70	37	87	69	92	18			
144	138	88	93	51	99			
137	66	94	90	80	150			
14	135	129	77	28				

Figure 4: Experimental design. Each plot is represented by provenance number. Block 1 is in grey, block 2 is in orange and block 3 is in green.

Table 1: List of provenances established at Rånna trail site, sorted by provenance number

Prov no.	Name	Country ( - region)	Number of trees sampled*	Long	Lat	Alt (m a.s.l.)
11	F.D des Charmettes	FR	32	45.60	2.68	900
14	F.D de Lagast	FR	45	44.15	2.63	850
26	Glorup	DK	32	55.18	10.68	70
18	F.D de Ligny en Barrois	FR	41	48.62	5.27	350
28	Ryssberget	SE	29	56.08	14.60	90
36	Osterholz-Scharmbeck	DE - Lower Saxony	49	53.23	8.80	25
37	Deister	DE - Lower Saxony	20	52.25	9.50	175
38	Harsefeld	DE - Lower Saxony	41	53.30	9.53	43
39	Seelzerthurm	DE - Lower Saxony	48	51.80	9.70	360
40	Bovenden	DE - Lower Saxony	51	51.50	9.83	375
43	Busschewald	DE - Lower Saxony	32	53.23	10.52	75
44	Oderhaus	DE - Lower Saxony	44	51.67	10.83	710
51	Eitorf 1502/262a	DE - North-Rhine-Whestf.	14	50.77	7.45	305
66	Dillenburg	DE – Hesse	33	50.73	8.27	500
67	Hadamar	DE – Hesse	38	50.45	8.07	218
69	Büdingen Abt. 762 (Standard)	DE – Hesse	34	50.28	9.12	198
70	Büdingen Abt. 763 (Standard)	DE – Hesse	57	50.28	9.12	225
73	Sinntal Abt. 414 A (Standard)	DE – Hesse	43	50.32	9.63	465
77	Eisenach	DE – Thuringia	38	50.08	10.08	615
80	Ebeleben	DE – Thuringia	37	51.33	10.50	315
87	Osburg	DE - Rhineland-Palatinate	46	49.68	6.82	540
88	Morbach	DE - Rhineland-Palatinate	28	50.75	7.00	660
90	Kirchheimbolanden	DE - Rhineland-Palatinate	33	49.67	8.02	400
92	Elmstein-Süd, Appenthal	DE - Rhineland-Palatinate	26	49.37	7.95	405
93	Montbaur	DE - Rhineland-Palatinate	37	50.43	7.83	313
94	Etterheim	DE - Baden-Wurtenberg	28	48.20	7.92	445
99	Ehingen	DE - Baden-Wurtenberg	30	48.40	9.50	620
104	Zwiesel	DE - Bavaria	37	49.02	13.23	755
129	Smolenice	SK	28	48.48	17.37	280
130	Trenčín	SK	32	48.88	18.00	200
135	Medzilaborce-Koškovce	SK	36	49.28	21.83	370
137	Postojna	SI	49	45.75	14.32	1100
138	Rogaska Slatina	SI	31	46.30	15.60	420
144	Rachiv	UA	38	48.04	24.17	520
150	Sovata (25)	RO	25	46.58	25.00	1015
161	Fläming	DE - Saxony-Anhalt	44	52.13	12.58	135

\* The number of sampled trees represent all living trees in March 2020.

Table 2: Provenance stand characteristics: Number of stems per hectare (N/ha), Basal Area (BA) and Survival

Prov. no.	Name	Country ( - region)	N/ha	BA (m <sup>2</sup> /ha)	Survival (%)**
11	F.D des Charmettes	FR	1067	12.56	21.33
14	F.D de Lagast	FR	1500	14.76	30.00
26	Glorup	DK	1067	13.59	21.33
18	F.D de Ligny en Barrois	FR	1367	17.06	27.33
28	Ryssberget	SE	967	10.87	19.33
36	Osterholz-Scharmbeck	DE - Lower Saxony	1633	16.90	32.67
37	Deister	DE - Lower Saxony	667	13.50	13.33
38	Harsefeld	DE - Lower Saxony	1367	15.85	27.33
39	Seelzerthurm	DE - Lower Saxony	1600	22.68	32.00
40	Bovenden	DE - Lower Saxony	1700	19.21	34.00
43	Busschewald	DE - Lower Saxony	1067	12.11	21.33
44	Oderhaus	DE - Lower Saxony	1467	14.23	29.33
51	Eitorf 1502/262a	DE - North-Rhine-Whestf.	467	5.17	9.33
66	Dillenburg	DE - Hesse	1100	15.47	22.00
67	Hadamar	DE - Hesse	1267	14.85	25.33
69	Büdingen Abt. 762 (Standard)	DE - Hesse	1133	11.54	22.67
70	Büdingen Abt. 763 (Standard)	DE - Hesse	1900	20.88	38.00
73	Sinntal Abt. 414 A (Standard)	DE - Hesse	1433	16.17	28.67
77	Eisenach	DE - Thuringia	1267	14.45	25.33
80	Ebeleben	DE - Thuringia	1233	15.08	24.67
87	Osburg	DE - Rhineland-Palatinate	1533	16.19	30.67
88	Morbach	DE - Rhineland-Palatinate	933	12.79	18.67
90	Kirchheimbolanden	DE - Rhineland-Palatinate	1100	12.65	22.00
92	Elmstein-Süd, Appenthal	DE - Rhineland-Palatinate	867	11.12	17.33
93	Montbaur	DE - Rhineland-Palatinate	1233	12.72	24.67
94	Etterheim	DE - Baden-Wurtenberg	933	13.87	18.67
99	Ehingen	DE - Baden-Wurtenberg	1000	13.25	20.00
104	Zwiesel	DE - Bavaria	1233	10.00	24.67
129	Smolenice	SK	933	12.77	18.67
130	Trenčín	SK	1067	14.46	21.33
135	Medzilaborce-Koškovce	SK	1200	10.55	24.00
137	Postojna	SI	1633	17.62	32.67
138	Rogaska Slatina	SI	1033	10.02	20.67
144	Rachiv	UA	1267	13.83	25.33
150	Sovata (25)	RO	833	11.05	16.67
161	Fläming	DE - Saxony-Anhalt	1467	15.48	29.33

\*\* Survival represents percentage of currently living trees out of initial 5000 trees per hectare planted in 1995. The stand was (pre-commercially) thinned twice and some trees also died spontaneously (self-thinning).

## 3.2. Data collection

Current data was collected in March 2020, that is, twelve years after the last inventory, and twenty-five years after the establishment. Stand plot measurements were recorded as listed below.

### **Diameter at breast height (DBH) and basal area increment (BAI)**

DBH was measured for all living trees ( $n = 1306$ ). BAI was calculated as a difference between individual tree basal areas in 2008 and 2020 divided by number of growing seasons between inventories.

**Tree height (H) and height increment (HI).** Tree height was measured for 108 randomly selected trees, including one tree per plot (three trees per provenance). Based on the H-DBH relationship, it was possible to estimate heights for all living trees.

**Crookedness.** Stem crookedness was evaluated from two perpendicular sides; the tree was classified using the following scale:

1 = straight, the tree was straight from both observation points

2 = slightly crooked; the stem was straight from one observation point and crooked from the second observation point

3 = significantly crooked; the tree was significantly crooked without any straightness seen from both observation points.

**Classification of stem morphology.** This parameter refers to the morphological appearance of a tree and to the tendency of a tree to branch and present bifurcated stems. We can distinguish 5 main classes:

class 1: straight (continuous) main stem

class 2: not continuous main stem but negligible reduction in height growth

class 3: bifurcated trunk with a bifurcation point above 1.3 m above the ground

class 4: bifurcated trunk with a bifurcation point below 1.3 m above the ground

class 5: bush- tree habitus with branches branched by the ground

class 6: wolf trees. Monumental trees that, by their appearance, height and volume, far exceed other trees.

**Spike knots.** Spike knots are appearing as a result of acutely angled branches. Branches, which were formed in a steep angle given on a stem, thus creating spike knots, might reduce the value of timber, since such timber is usually not suitable for peeling or some sawn products. Spike knots may also develop based on genetical predispositions of certain provenances. Spike knots are unwanted stem

harm, which may lead to reduced quality and significantly reduced timber price on the market. Spike knots were divided into two categories: below 0.5 meters and above 0.5 meters. For each tree, the number of spike knots was counted (Interpine Innovation 2021).

### 3.3. Data preparation

#### **Basal area increment**

Based on pairwise comparison of values measured in 2008 and 2020, tree basal area increment ( $\text{cm}^2/\text{year}$ ) was calculated (Table 3). The best random structure for the model resulted in plot nested to block effect (block/plot).

#### **Height increment**

Due to practical reasons and following common methods in the national forest inventories, height was measured only for approx. one tenth of all living trees. The individual tree height was estimated using a logarithmic regression model adjusted *ad-hoc*:

$$H_{20} = 81.587 * \ln(\text{DBH}_{20}) - 259.86.$$

After calculating height of each remaining tree, it was possible to calculate height increment as a difference between the values  $H_{20}$  and  $H_{08}$  (heights in 2020 and 2008 respectively). Tree height annual increment was then obtained as height increment divided by the number of years between the inventories. The final model used for height reconstruction is also shown in Appendix 1 - Supplementary figure 1.

#### **Crookedness**

Stem crookedness evaluation was made out depending on level of predisposition of trees to be crooked, ranging on scale 1, 2 or 3. More detailed description is shown in chapter 3.2. For this variable, generalized linear mixed model comprising Poisson error distribution was used. Thus, differences among beech provenances were considered in the model and only block was represented in the random structure.

#### **Classification of stem morphology**

For this variable, Poisson distribution was used. It was decided to exclude class 6, since it was very rare in the experiment and was usually only found on the edge trees in buffer zone.

### Spike knots above 0.5 m and spike knots below 0.5 m

Spike knots as indicator of timber quality were evaluated in the manuscript. For these variables, a generalized linear mixed model was used, including block as the unique random effect factor.

## 3.4. Statistical analysis

The response variables analyzed in this study are described in Table 3.

Table 3: Description of response variables evaluated

Dependent variable ( $y_{ijk}$ )	Description	Abbreviation	Error distribution	Variable type
Basal area increment & DBH	cm <sup>2</sup> /year & cm (2020)	BAI	Normal	Continuous
Height increment	cm/year	HI	Normal	Continuous
Stem crookedness	Range 1 – 3	Crook	Poisson	Count
Classification of stem morphology	Trees divided into 6 classes based on habitus	Class	Poisson	Count
Spike knots above 0.5 m	Amount of spike knots above 0.5 m	SpikeA	Poisson	Count
Spike knots below 0.5 m	Amount of spike knots below 0.5 m	SpikeB	Poisson	Count

Differences between European beech provenances on each of former variables were checked using Generalized (GLMM) or simple Linear Mixed Model (LMM). These models allow to consider spatial dependence of measurements via the use of random and fixed structure. The best random-effect structure was fitted by restricted maximum log-likelihood techniques (REML) and the goodness-of-fit of the different models was compared by means of Akaike information criterion (Zuur *et al.*, 2009). Nested random structures were used for plot nested in block. The fixed part of the model included provenance as unique explanatory variable and the final model was fitted by using REML. Differences between provenances for each response variable were evaluated using the following model:

$$y_{ijk} = \alpha_0 + \alpha_1 * \text{Provenance} + w_k + u_{jk} + \varepsilon_{ijk}$$

where  $\alpha_0$  and  $\alpha_1$  are intercept and coefficient associated to each other provenance. Subscript and parameters are explained in Table 4.

Table 4: Model variable description

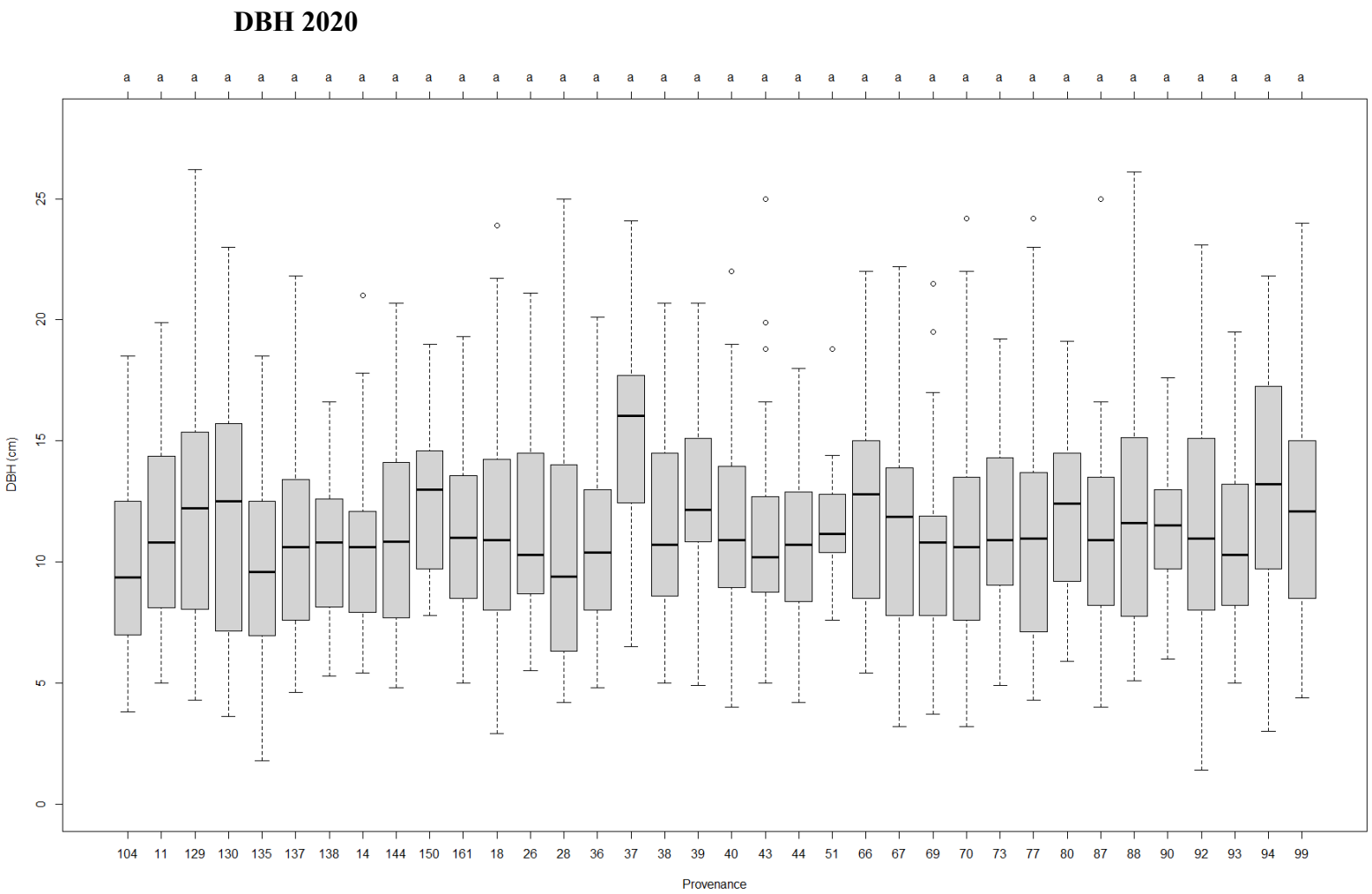
variable	Description
$y_{ijk}$	dependent variable
$i$	Tree
$j$	Plot
$k$	Block
Provenance	independent variable
$w \sim N(0, \sigma_k)$	block random effect
$u \sim N(0, \sigma_{jk})$	plot random effect
$\varepsilon_{ijk} \sim N(0, \sigma_e)$	error term

A Tuckey *post-hoc* analysis was used to identify pair provenances differences and obtain letters of significance for each studied response variables (Gramm *et al.* 2007).

Statistical analysis was conducted in RStudio version 4.1.1. (2021). Packages used for data evaluation were “multcomp” (Multiple Comparison package - Hothorn *et al.* 2008) and “nlme” (Non-linear Mixed Effects package - Pinheiro *et al.* 2015).



## 4. Results



*Figure 5: Diameter at breast height, 2020. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance*

Highest average DBH 2020 was found within provenance number 37 (Deister – DE – Lower Saxony). Usually, mean tree DBH varied approximately in 10 cm, with

extend between 7 and 13 cm (Figure 5). Minimal DBH was approx. 5 cm and, on the other hand, some trees exceeded DBH of 25 cm.

### Basal area increment ( $\text{cm}^2/\text{year}$ )

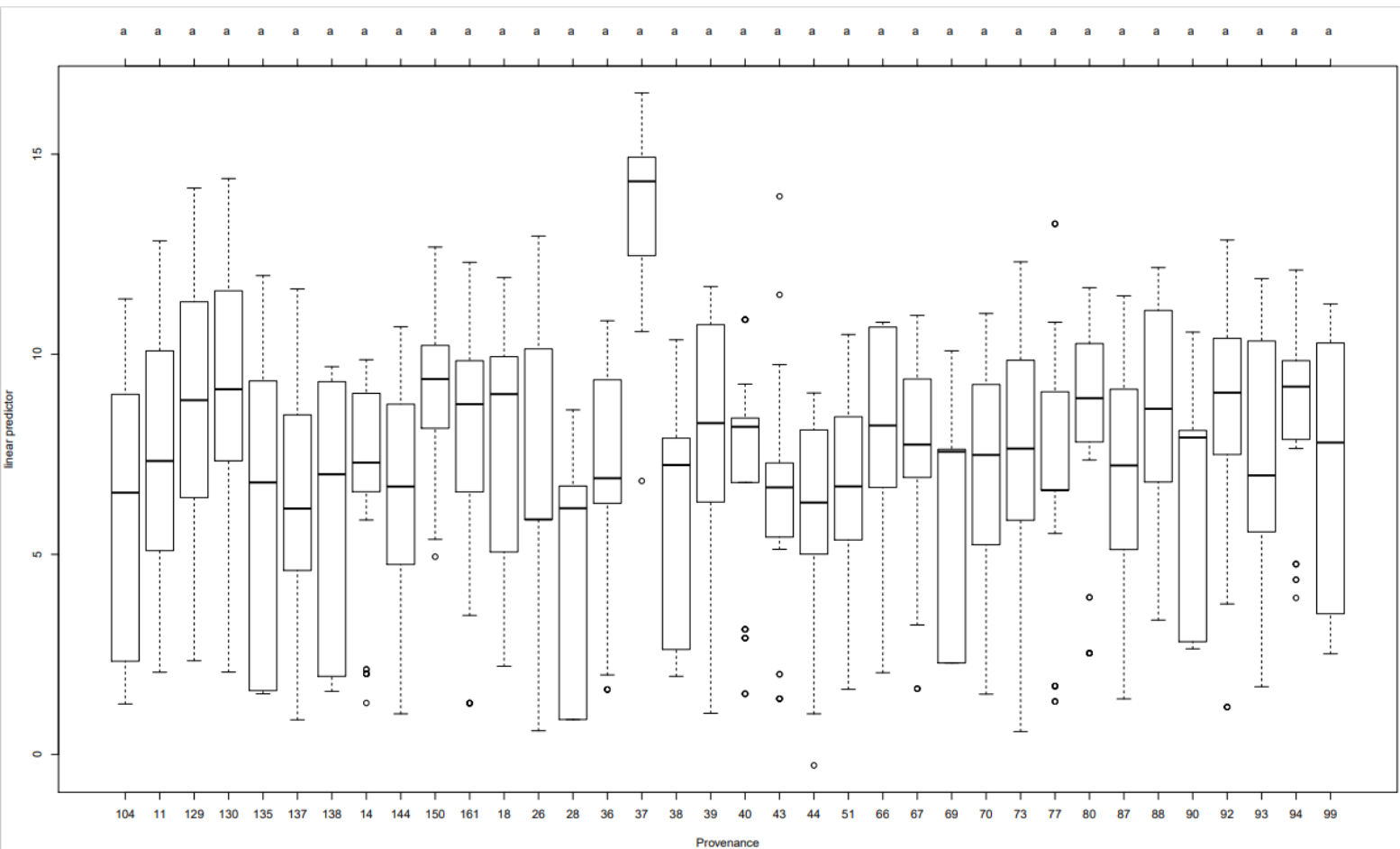


Figure 6: Basal area increment ( $\text{cm}^2/\text{year}$ ). Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance. The linear predictor (y axis) indicates the values of BAI ( $\text{cm}^2/\text{year}$ )

The only significant letter “a” confirms that no statistical differences in basal area increment were found (the confidence interval of all provenances overlaps). The mean value of BAI oscillates between 5 and 10  $\text{cm}^2$  per year (Figure 6). We can also observe a trend, that provenance number 37 (Deister – DE – Lower Saxony) has the highest BAI. Model results, i.e., coefficient and p-values can be consulted in Appendix 2 -Supplementary Table S1.

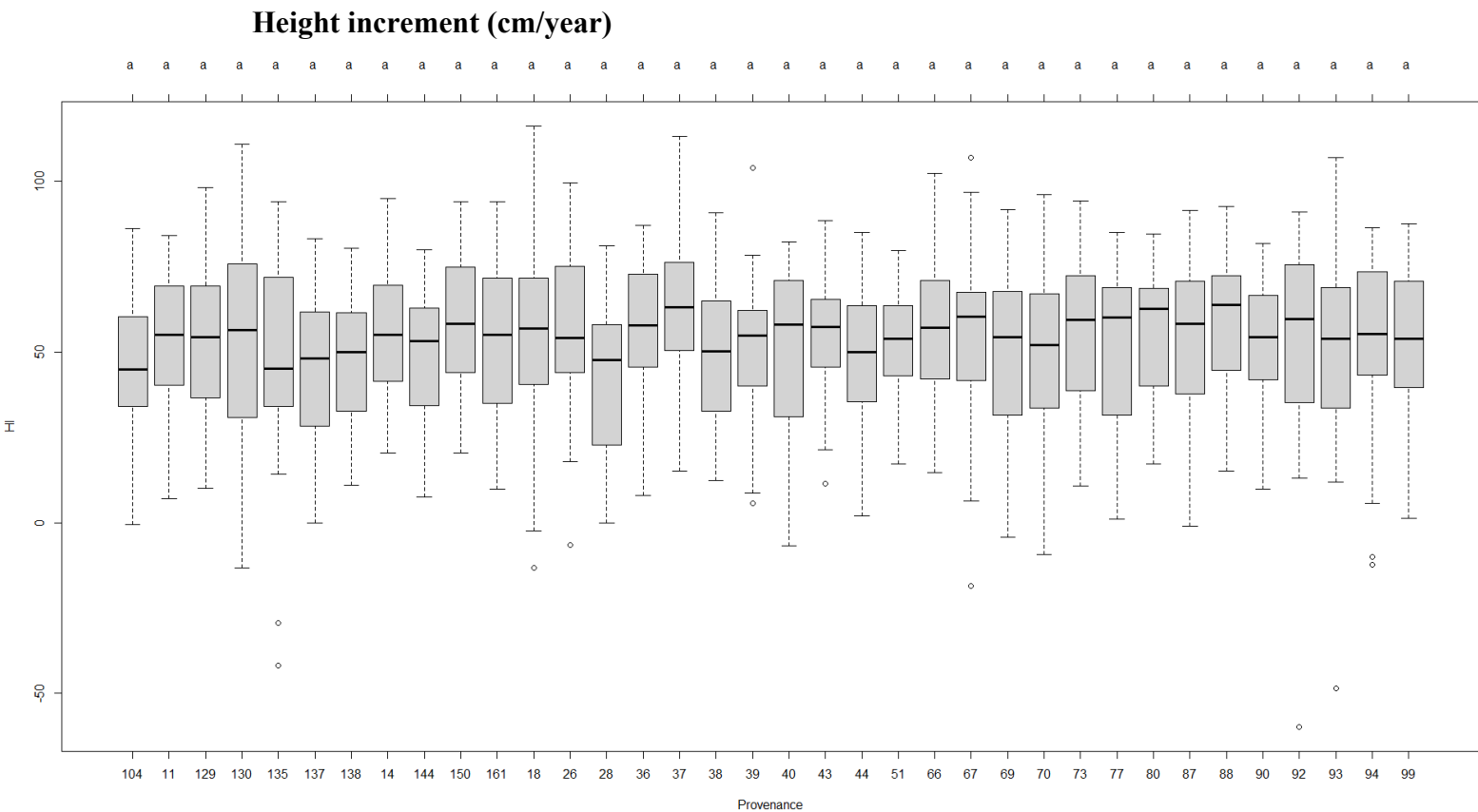


Figure 7: Height increment (cm/year). Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance. The y axis indicates HI (cm/year)

Mean stand height for 2020 was 13.1 m (number of trees sampled = 108; Appendix 1 - Supplementary Figure S2). Mean annual tree height increment was 0.3 m per year (1995 – 2001) and 0.5 m per year in the time of 2002 – 2008 (Skogforsk 2009). Height increment between last two inventories was calculated by height-diameter relationship fitted model, which can be found in Appendix 1 – Supplementary figure S1. Height increment varied from 40 to 70 cm per year (Figure 7, Appendix 2 – Supplementary table S2). Only small differences between provenances were found, probably due to thinning interventions previously done. Lowest height increment was found by provenance number 28 (Ryssberget – SE); greatest height increment was found by provenance number 37 (Deister – DE – Lower Saxony).

## Crookedness

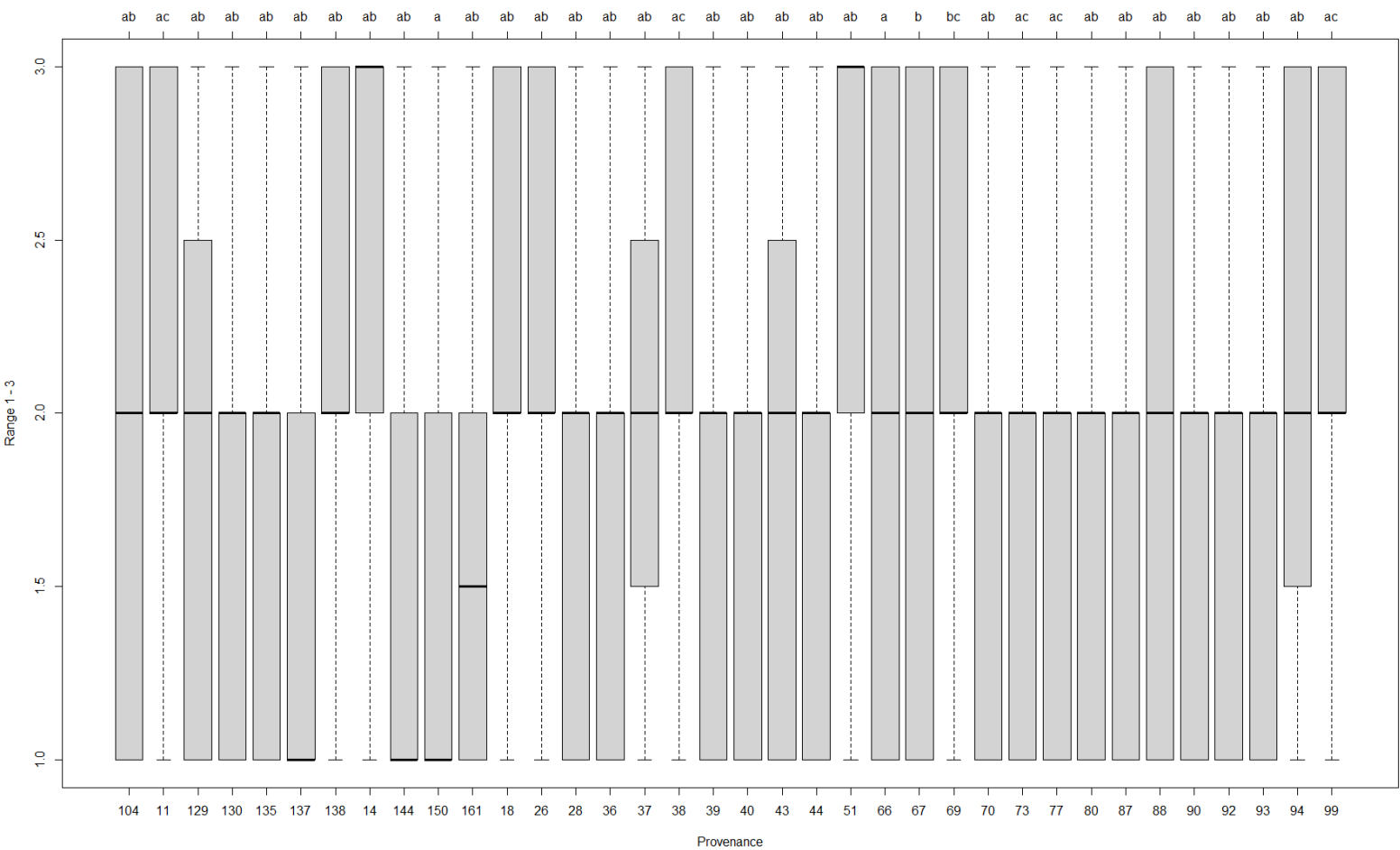


Figure 8: Crookedness. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance

High quality stems were found by southeastern European provenances 137 (Postojna – SI), 144 (Rachiv – UA) and 150 (Sovata (25) – RO). Most of the other provenances showed just somewhat fair quality, ranging between 1 and 2 (Figure 8, Appendix 2 – Supplementary Table S3). Only within provenances number 14 (F.D. des Charmettes - FR) and 51 (Eitorf 1502/262a – DE - North-Rhine-Whestf), most of trees are crooked from both sides.

## Classification of stem morphology

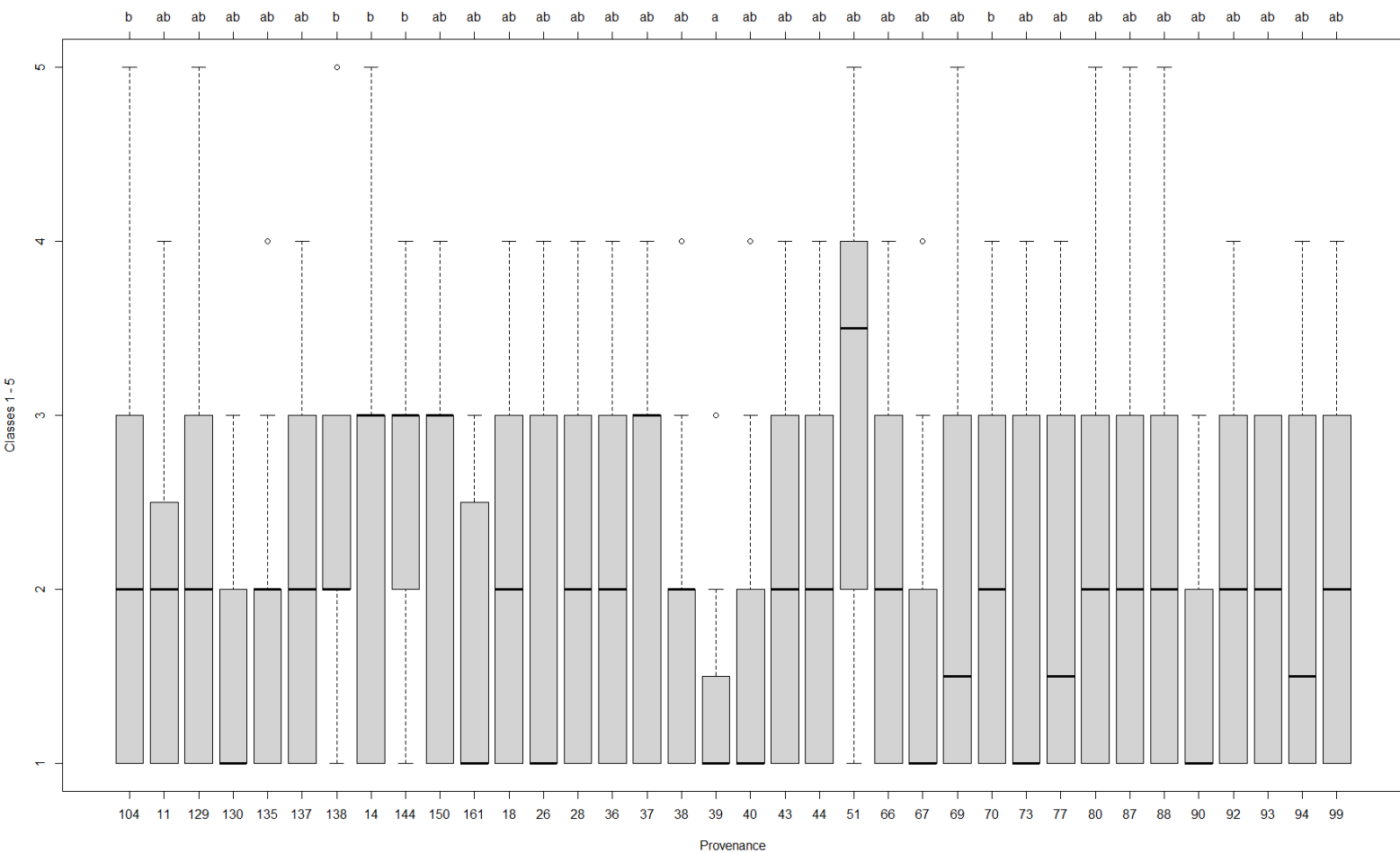


Figure 9: Classification of stem morphology. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance

The Figure 9 shows, that classification number 1 (straight (continuous) main stem), 2 (not continuous main stem but negligible reduction in height growth), and 3 (bifurcated trunk with a bifurcation point above 1.3 m above the ground) was mainly observed. For classification number 4 (bifurcated trunk with a bifurcation point below 1.3 m above the ground), rather rare samples were found. Provenance 39 (Seelzerthurm – DE – Lower Saxony) showed best results – only minority of trees were assigned to the classification number 2 and 3; on the contrary, most of the trees within provenance 39 belong to the class 1 (Appendix 2 – Supplementary Table S4). The worst class was found in case of provenance number 51 (Eitorf 1502/262a – DE - North-Rhine-Westfalia), indicating shrubby trees or trees which are bifurcating under 1.3 meters above the ground.

### Spike knots above 0.5 meters

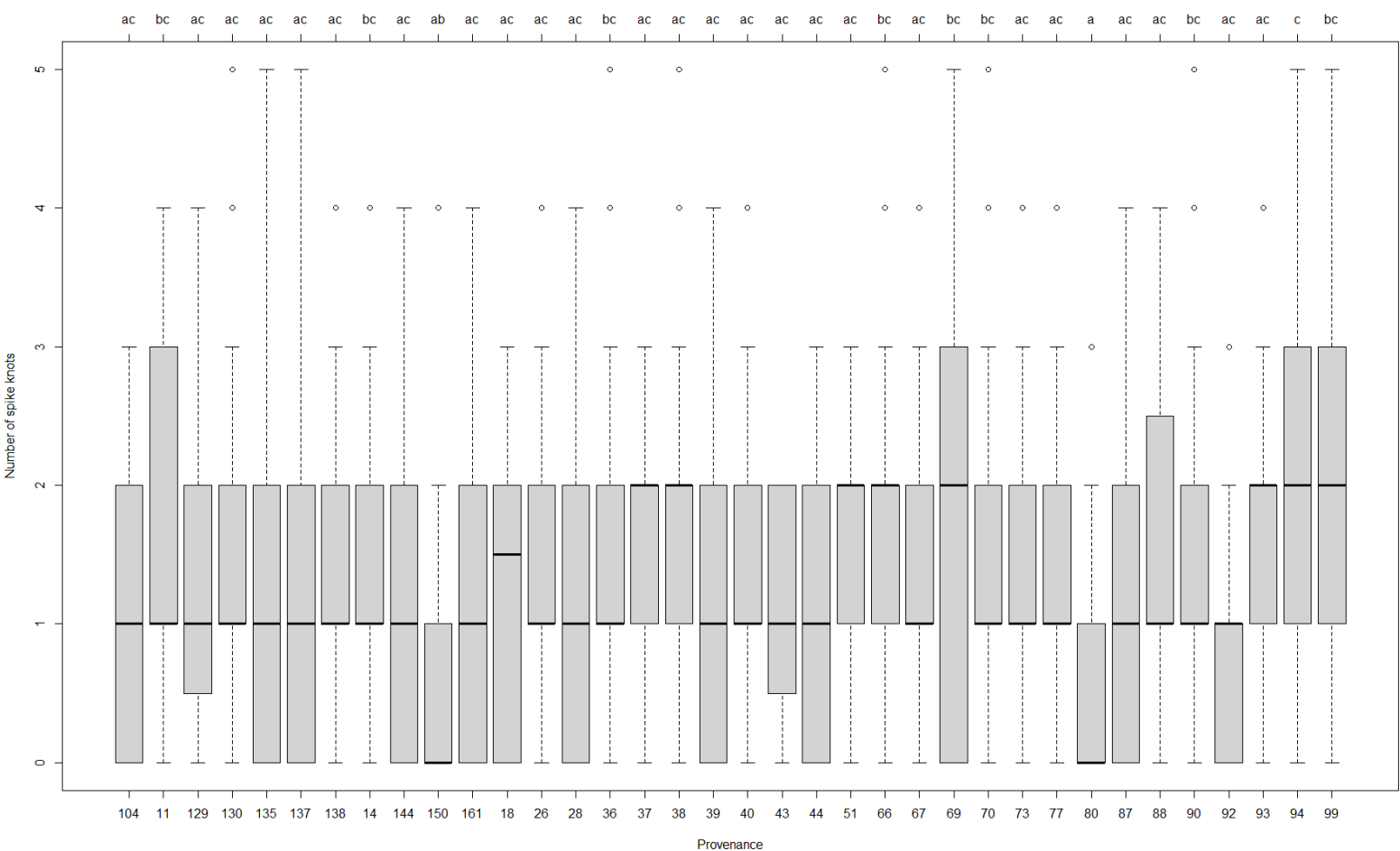


Figure 10: Spike knots above 0.5 meters. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance

Figure 10 shows, that provenance with lowest amount of spike knots was number 80 (Ebeleben, DE-Thuringia) and number 150 (Sovata – RO). These provenances differed from the rest because no tree with three and more spike knots above 0.5 m was found (Figure 10). Usually, trees showed similar patterns belonging to the spike knots quantity 1 to 2. Provenances number 11 (F.D des Charmettes – FR), 14 (F.D. de Lagast – FR), 66 (Dillenburg – DE-Hesse), 69 (Büdingen Abt. 762 – DE-Hesse), 70 (Büdingen Abt. 763 – DE -Hesse), 90 (Kirchheimbolanden – DE- Rhineland-Palatinate) and 99 (Ehingen – DE - Baden-Wurtenberg) were distinguished by higher quantity of spike knots. Provenance 94 (Ettreheim – DE – Baden-Wuttenberg) with the letter of significance “c” showed the worst possible

qualitative characteristic of the evaluated variable (Appendix 2 – Supplementary Table S5).

### Spike knots below 0.5 meters

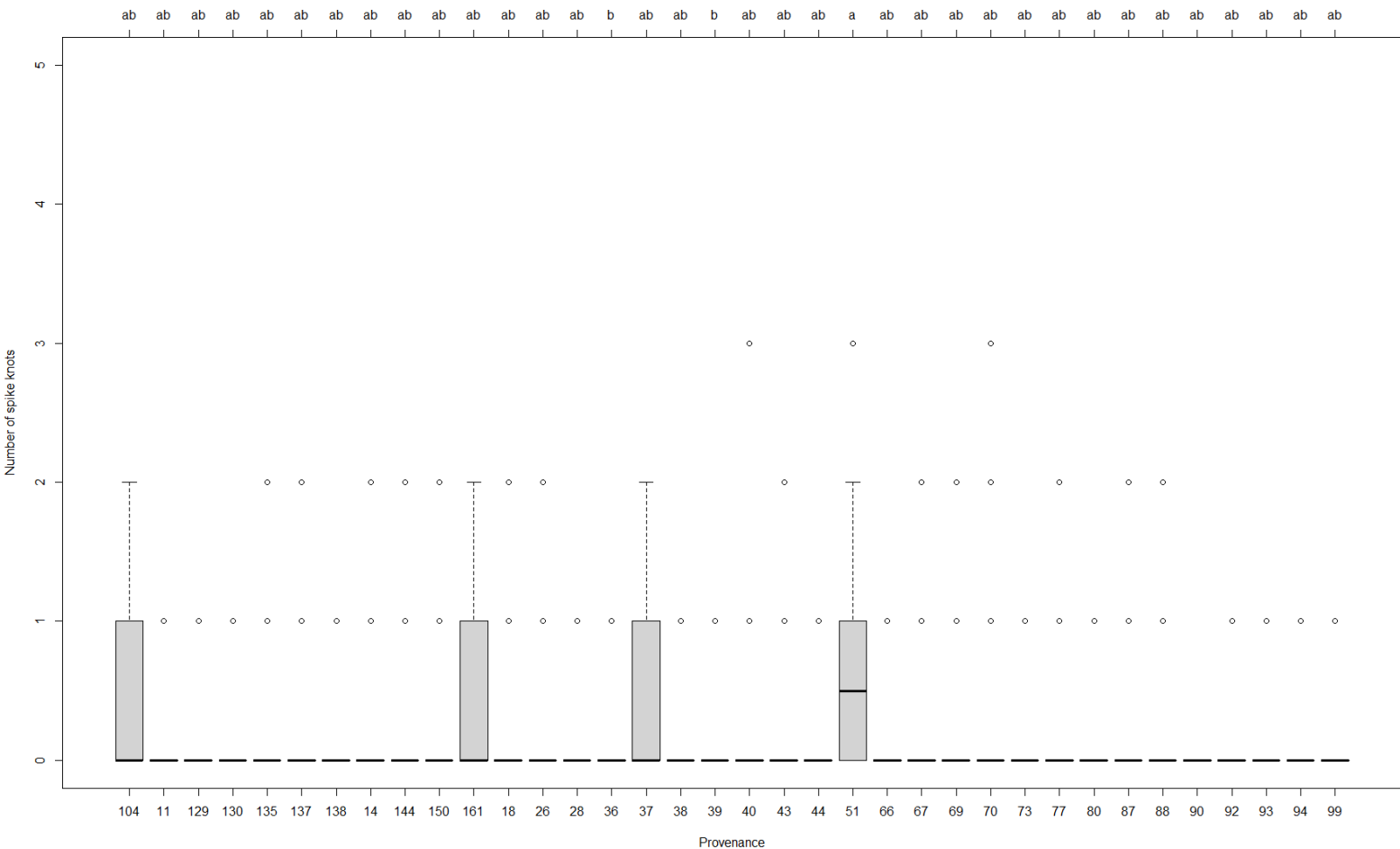


Figure 11: Spike knots below 0.5 meters. Different letters denote significant differences at 0.05 significance level. The black lines indicate the mean value for the specific provenance

Only four German provenances originating from different region of the country showed number of spike knots ranging between 0 and 1 (Figure 11). To be named: Provenance number 37 (Deister – Lower Saxony), 51 (Eitorf 1502/262a – North-Rhine-Whestfalia), 104 (Zwiesel – Bavaria) and 161 (Flaming - Saxony–Anhalt). Two provenances originating from Lower Saxony, Germany (number 36 – Osterholz-Scharmbeck and number 39 – Seelenthurm), labelled by “b” significance letter, showed the best results of the evaluated variable (Appendix 2 – Supplementary Table S6). For the rest of provenances, almost no spike knots under 0.5 m was observed.

## 5. Discussion

In this study, we tested the tree growth and timber characteristics between several European beech provenances coming from a wide area of the European continent. We provided insights into the more adequate provenances to improve production and timber quality which could serve as guideline for designing forest management decisions in Sweden. We observed no significant differences between provenances in terms of tree basal area or height growth between the last two inventories. Therefore, our first and second hypothesis were rejected. We could not evidence any growth advantage for the southern European or local Swedish provenances. However, we observed that the German provenance number 37 (Deister, Lower Saxony) showed a higher growth trend for tree basal area, height increment and total height compared to the rest of provenances. We hypothesize that those differences could become greater and, hence, significant in future inventories. Thus, we may consider that provenance as the most interesting one with remarkable potential for future use in Sweden for a timber production proposal.

Results from other experimental provenance trials established in southern Sweden showed similar to those presented here. Bergkvist (2019) evidenced no difference in tree growth between European beech provenances in southern Sweden, but a good performance for native Swedish ones. Previous inventories for the same experimental site studied here, showed that German provenances presented higher basal area increment compared to the others (Skogforsk 2009). Accordingly, in the last inventory carried out in 2008, the German provenance number 39 showed the best performance regarding tree growth. Ježík *et al.* (2016) concluded that the lowest tree growth is commonly found for the provenance from the most oceanic climate and lowest altitude. In addition, site characteristic could influence tree height growth depending on provenance of origin (Stojnic *et al.* 2010). Future research and new stand inventories in the present experimental trial would be essential to provide a better understanding of the European beech provenances differences on tree growth characteristics.

Timber quality differences were observed between provenances regarding the second goal of the present work. South-eastern provenances were found to present the lowest crookedness and spike knots above 0.5 m, although central European ones were equally adequate in similar studies in Sweden (Bergkvist 2019). German



provenances (number 39 and 37) showed good timber qualities such as the lowest tendency to develop double stems and spike knots below 0.5 m. However, the worst provenance according to timber quality was German too (number 51), which agree with similar studies in southern Sweden (Bergkvist 2019). It evidenced that even neighboring provenances could show more different adaptive traits compared to distant ones (Rau *et al.* 2015). Accordingly, a high genetic diversity within provenances has been frequently revealed (Muller *et al.* 2016). German provenance number 51 was observed economically the less valuable and might be mainly considered only for firewood use. Denser initial spacing may be recommended to reduce the likelihood of low branching and to promote height growth for that provenance. Native provenances from Sweden and Denmark showed generally good timber qualities compared to the rest of provenances. In this sense, Bergkvist (2019) evidenced that they rarely trend to bifurcation.

The experimental trial studied here might be used onwards to test the response of different European beech provenances to the ongoing climate change. Drought adaptation might play an important role for seedlings survival, tree growth and timber quality. This adaptation could limit growth and timber performance, since biomass distribution, leaf and root system morphology are evidently a core strategy of beech saplings to cope with water deficits (Knutzen *et al.* 2015). Provenances from continental to subcontinental climate, with higher probability of summer droughts occurrence, present several functional traits for a well drought adaptation compared to the sub-oceanic Central Germany (Rose *et al.* 2009). In this sense, we could expect a good drought adaptation for provenance number 40 (Boveden) in the experimental site studied here. A low drought response was also found in sandy soils for European beech (Buhk *et al.* 2016). It may be capable to face more frequent drought episodes from climate change by stomatal density changes (Stojnic *et al.* 2015), what would be interesting to compare the response of different European beech provenances in the future. Banach *et al.* (2015) evidenced that natural beech population growing in difficult environments showed better growing patterns in sites with arduous conditions such as higher altitudes. On the other hand, extreme winter frost from climate change could be similarly important than drought (Czajkowski *et al.* 2006b), what could be evaluated in future researches.

The results presented here may be limited by inherent features related with the experimental design. Stands were thinned two times after establishment. This could homogenize growth and timber features among provenances removing dominated and malformed trees, influencing also tree survival. Some standing trees were damaged accidentally by thinning treatment which could affect growth and timber quality. Strip roads might influence stem crookedness, enhancing growth of lateral branches and trunk tilt. Despite a buffer zone to avoid interactions from other factors unrelated with the experiment, the closeness to an adjacent old forest may

affect in different way tree growth of provenances due to wind protection or sunlight interception. Differences in soil types and high mortality related to waterlogging (beech was replaced by natural regeneration of black alder- *Alnus glutinosa* (L.) Gaertn.) could affect observed results (Gömöry *et al.* 2011). Spike knots, especially those below 0.5 m, were hard to observed and, hence, to evaluate. There are no universal international restoration programs, so each region of provenance has different marketing rules (Auñon *et al.* 2011). Magagna *et al.* (2020) reminds, that foresters should pay attention to the forest management documentation, only then they can keep quality sources of reproductive planting material and separate them from malleable, low-quality sources.

Results of the manuscript provide a scientific basis to select the right provenance if the timber quality is the management goal. European beech promotion, to the detriment of Norway spruce in southern Sweden, may involve positive non-timber outcomes, such as enhance biodiversity via increasing broadleaved forest, recreational and other ecosystem services.

## 6. Conclusions

The aim of this thesis was to examine tree growth and timber quality differences among European beech provenances in Sweden. The study showed that, despite no significant differences on tree growth, German provenance number 37 (Deister, Lower Saxony) revealed an important potential for high quality timber production. In addition, German provenance number 39 (Seelzerthurm, Lower Saxony) had the lowest tendency to develop double stems and spike knots below 0.5 m. Another interesting provenance was a Romanian provenance number 150 (Sovata (25)) with the lowest values of crookedness and number of spike knots above 0.5 m. Swedish and Danish beech provenances, which were hypothesized to express high growth rates, since they are naturally adapted to Nordic conditions, did not differ significantly from other provenances.

The results of this study indicate that the genetic background of the studied provenances could have an important role on tree growth and timber quality features of European beech. However, more research and future inventories is needed to clarify the tree growth differences between provenances. In addition, the experimental design described here may be used to improve the current understanding of European beech adaptation to face the ongoing climate change in Southern Sweden.

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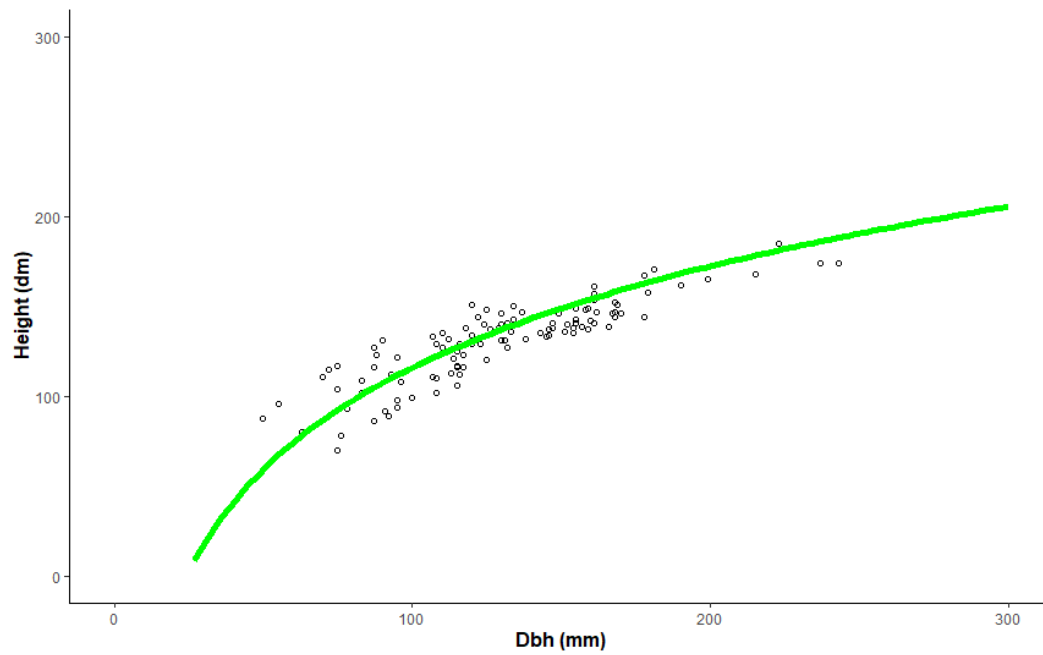
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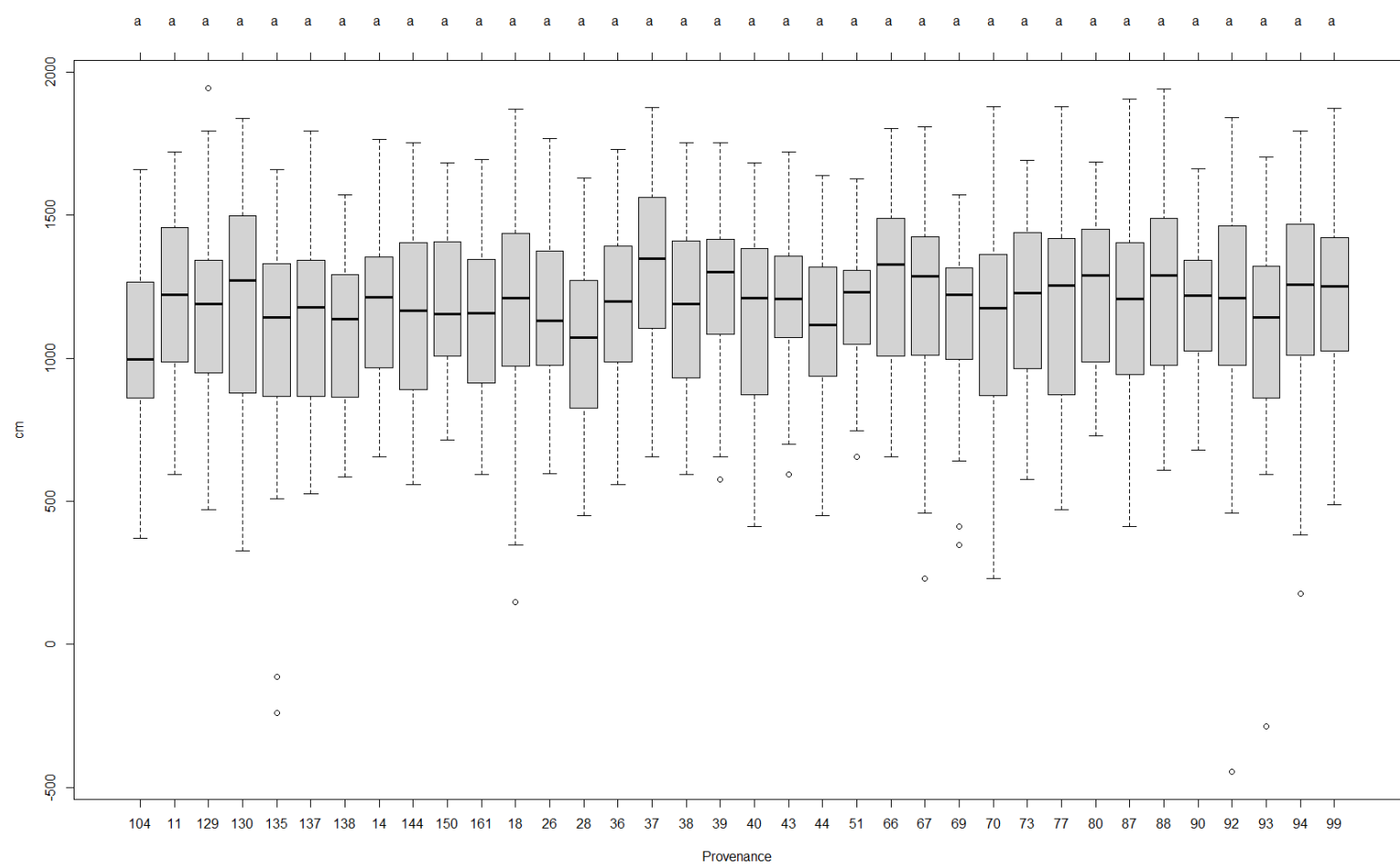
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## Appendix 1 - supplementary figures



*Supplementary Figure S1: The height - diameter relationship fitted model*



*Supplementary Figure S2: Total height, 2020*

## Appendix 2 – supplementary tables

*Supplementary Table S1: Model-fitted coefficients for Basal Area Increment*

Parameter	Coefficient	p-value
$\alpha_0$ (Provenance 104)	5.576	0.0000
$\alpha_1$ (Provenance 11)	0.717	0.4754
$\alpha_1$ (Provenance 129)	1.746	0.0854
$\alpha_1$ (Provenance 130)	1.854	0.0681
$\alpha_1$ (Provenance 135)	0.266	0.7907
$\alpha_1$ (Provenance 137)	-0.115	0.9082
$\alpha_1$ (Provenance 138)	-0.385	0.7014
$\alpha_1$ (Provenance 14)	-0.523	0.6026
$\alpha_1$ (Provenance 144)	-0.407	0.6850
$\alpha_1$ (Provenance 150)	0.410	0.6826
$\alpha_1$ (Provenance 161)	0.159	0.8736
$\alpha_1$ (Provenance 18)	1.130	0.2623
$\alpha_1$ (Provenance 26)	1.169	0.2462
$\alpha_1$ (Provenance 28)	-0.383	0.7023
$\alpha_1$ (Provenance 36)	0.230	0.8188
$\alpha_1$ (Provenance 37)	3.004	0.0037
$\alpha_1$ (Provenance 38)	0.454	0.6512
$\alpha_1$ (Provenance 39)	0.874	0.3852
$\alpha_1$ (Provenance 40)	0.346	0.7300
$\alpha_1$ (Provenance 43)	0.480	0.6323
$\alpha_1$ (Provenance 44)	-0.910	0.3661
$\alpha_1$ (Provenance 51)	-0.290	0.7725
$\alpha_1$ (Provenance 66)	1.154	0.2522
$\alpha_1$ (Provenance 67)	1.168	0.2469
$\alpha_1$ (Provenance 69)	0.336	0.7377
$\alpha_1$ (Provenance 70)	0.226	0.8214
$\alpha_1$ (Provenance 73)	0.352	0.7256
$\alpha_1$ (Provenance 77)	0.564	0.5741
$\alpha_1$ (Provenance 80)	0.448	0.6555
$\alpha_1$ (Provenance 87)	0.083	0.9335
$\alpha_1$ (Provenance 88)	1.972	0.0526

$\alpha_1$ (Provenance 90)	0.253	0.8006
$\alpha_1$ (Provenance 92)	0.944	0.3481
$\alpha_1$ (Provenance 93)	0.528	0.5990
$\alpha_1$ (Provenance 94)	1.892	0.0627
$\alpha_1$ (Provenance 99)	1.752	0.0843

*Supplementary Table S2: Model-fitted coefficients for Height Increment*

Parameter	Coefficient	p-value
$\alpha_0$ (Provenance 104)	12.131	0.0000
$\alpha_1$ (Provenance 11)	0.609	0.5439
$\alpha_1$ (Provenance 129)	0.608	0.5446
$\alpha_1$ (Provenance 130)	1.221	0.2261
$\alpha_1$ (Provenance 135)	-0.047	0.9626
$\alpha_1$ (Provenance 137)	-0.328	0.7438
$\alpha_1$ (Provenance 138)	-0.098	0.9218
$\alpha_1$ (Provenance 14)	1.240	0.2189
$\alpha_1$ (Provenance 144)	0.225	0.8222
$\alpha_1$ (Provenance 150)	2.021	0.0471
$\alpha_1$ (Provenance 161)	0.812	0.4194
$\alpha_1$ (Provenance 18)	0.949	0.3459
$\alpha_1$ (Provenance 26)	1.624	0.1088
$\alpha_1$ (Provenance 28)	-0.599	0.5509
$\alpha_1$ (Provenance 36)	1.455	0.1499
$\alpha_1$ (Provenance 37)	2.406	0.0188
$\alpha_1$ (Provenance 38)	0.208	0.8352
$\alpha_1$ (Provenance 39)	0.658	0.5123
$\alpha_1$ (Provenance 40)	0.525	0.6009
$\alpha_1$ (Provenance 43)	1.151	0.2534
$\alpha_1$ (Provenance 44)	0.244	0.8073
$\alpha_1$ (Provenance 51)	0.676	0.5010
$\alpha_1$ (Provenance 66)	1.338	0.1850
$\alpha_1$ (Provenance 67)	1.194	0.2363
$\alpha_1$ (Provenance 69)	0.402	0.6888
$\alpha_1$ (Provenance 70)	0.297	0.7673
$\alpha_1$ (Provenance 73)	1.273	0.2072
$\alpha_1$ (Provenance 77)	0.495	0.6221
$\alpha_1$ (Provenance 80)	1.377	0.1727
$\alpha_1$ (Provenance 87)	1.070	0.2880
$\alpha_1$ (Provenance 88)	1.833	0.0711

$\alpha_1$ (Provenance 90)	0.706	0.4821
$\alpha_1$ (Provenance 92)	0.949	0.3455
$\alpha_1$ (Provenance 93)	0.445	0.6576
$\alpha_1$ (Provenance 94)	1.034	0.3044
$\alpha_1$ (Provenance 99)	1.033	0.3049

*Supplementary Table S3: Model-fitted coefficients for Crookedness*

Parameter	Coefficient	p-value
$\alpha_0$ (Provenance 104)	-1.024	0.3060
$\alpha_1$ (Provenance 11)	-1.942	0.0521
$\alpha_1$ (Provenance 129)	-1.028	0.3040
$\alpha_1$ (Provenance 130)	-0.836	0.4032
$\alpha_1$ (Provenance 135)	-0.435	0.6636
$\alpha_1$ (Provenance 137)	1.063	0.2878
$\alpha_1$ (Provenance 138)	-1.583	0.1134
$\alpha_1$ (Provenance 14)	-2.705	0.0068
$\alpha_1$ (Provenance 144)	2.512	0.0119
$\alpha_1$ (Provenance 150)	2.010	0.0444
$\alpha_1$ (Provenance 161)	0.774	0.4389
$\alpha_1$ (Provenance 18)	-2.221	0.0263
$\alpha_1$ (Provenance 26)	-1.775	0.0758
$\alpha_1$ (Provenance 28)	0.016	0.9870
$\alpha_1$ (Provenance 36)	-0.990	0.3222
$\alpha_1$ (Provenance 37)	-1.191	0.2336
$\alpha_1$ (Provenance 38)	-1.538	0.1240
$\alpha_1$ (Provenance 39)	-0.336	0.7367
$\alpha_1$ (Provenance 40)	-0.924	0.3553
$\alpha_1$ (Provenance 43)	-1.107	0.2682
$\alpha_1$ (Provenance 44)	0.378	0.7056
$\alpha_1$ (Provenance 51)	-1.709	0.0873
$\alpha_1$ (Provenance 66)	-1.192	0.2332
$\alpha_1$ (Provenance 67)	-0.845	0.3983
$\alpha_1$ (Provenance 69)	-2.349	0.0188
$\alpha_1$ (Provenance 70)	-1.101	0.2707
$\alpha_1$ (Provenance 73)	-0.779	0.4358
$\alpha_1$ (Provenance 77)	0.305	0.7607
$\alpha_1$ (Provenance 80)	-0.054	0.9565
$\alpha_1$ (Provenance 87)	-0.383	0.7018
$\alpha_1$ (Provenance 88)	-0.439	0.6605



$\alpha_1$ (Provenance 90)	-0.663	0.5075
$\alpha_1$ (Provenance 92)	-0.827	0.4084
$\alpha_1$ (Provenance 93)	-1.252	0.2105
$\alpha_1$ (Provenance 94)	-1.328	0.1840
$\alpha_1$ (Provenance 99)	-2.084	0.0371

*Supplementary Table S4: Model-fitted coefficients for Classification of stem morphology*

Parameter	Coefficient	p-value
$\alpha_0$ (Provenance 104)	-2.628	0.0085
$\alpha_1$ (Provenance 11)	1.461	0.1440
$\alpha_1$ (Provenance 129)	0.184	0.8536
$\alpha_1$ (Provenance 130)	2.873	0.0040
$\alpha_1$ (Provenance 135)	1.777	0.0756
$\alpha_1$ (Provenance 137)	1.516	0.1295
$\alpha_1$ (Provenance 138)	-0.363	0.7163
$\alpha_1$ (Provenance 14)	0.449	0.6533
$\alpha_1$ (Provenance 144)	-0.272	0.7852
$\alpha_1$ (Provenance 150)	1.093	0.2743
$\alpha_1$ (Provenance 161)	2.806	0.0050
$\alpha_1$ (Provenance 18)	0.697	0.4859
$\alpha_1$ (Provenance 26)	2.434	0.0149
$\alpha_1$ (Provenance 28)	0.689	0.4907
$\alpha_1$ (Provenance 36)	1.339	0.1804
$\alpha_1$ (Provenance 37)	0.661	0.5085
$\alpha_1$ (Provenance 38)	1.753	0.0796
$\alpha_1$ (Provenance 39)	4.141	3.47e-05
$\alpha_1$ (Provenance 40)	3.022	0.0025
$\alpha_1$ (Provenance 43)	1.705	0.0882
$\alpha_1$ (Provenance 44)	1.891	0.0586
$\alpha_1$ (Provenance 51)	-0.899	0.3688
$\alpha_1$ (Provenance 66)	1.365	0.1721
$\alpha_1$ (Provenance 67)	2.225	0.0261
$\alpha_1$ (Provenance 69)	1.971	0.0487
$\alpha_1$ (Provenance 70)	0.958	0.3379
$\alpha_1$ (Provenance 73)	2.348	0.0188
$\alpha_1$ (Provenance 77)	2.018	0.0436
$\alpha_1$ (Provenance 80)	1.685	0.0919
$\alpha_1$ (Provenance 87)	0.791	0.4289

$\alpha_1$ (Provenance 88)	0.783	0.4333
$\alpha_1$ (Provenance 90)	2.074	0.0381
$\alpha_1$ (Provenance 92)	1.281	0.2003
$\alpha_1$ (Provenance 93)	1.467	0.1424
$\alpha_1$ (Provenance 94)	1.884	0.0595
$\alpha_1$ (Provenance 99)	1.144	0.2525

*Supplementary Table S5: Model-fitted coefficients for Spike knots above 0.5 m*

Parameter	Coefficient	p-value
$\alpha_0$ (Provenance 104)	1.693	0.0905
$\alpha_1$ (Provenance 11)	1.702	0.0888
$\alpha_1$ (Provenance 129)	0.031	0.9753
$\alpha_1$ (Provenance 130)	0.707	0.4792
$\alpha_1$ (Provenance 135)	-0.018	0.9852
$\alpha_1$ (Provenance 137)	-0.534	0.5932
$\alpha_1$ (Provenance 138)	1.121	0.2623
$\alpha_1$ (Provenance 14)	1.005	0.3147
$\alpha_1$ (Provenance 144)	-1.275	0.2023
$\alpha_1$ (Provenance 150)	-2.177	0.0294
$\alpha_1$ (Provenance 161)	-1.110	0.2668
$\alpha_1$ (Provenance 18)	0.067	0.9465
$\alpha_1$ (Provenance 26)	0.172	0.8637
$\alpha_1$ (Provenance 28)	-0.017	0.9861
$\alpha_1$ (Provenance 36)	1.156	0.2474
$\alpha_1$ (Provenance 37)	1.168	0.2428
$\alpha_1$ (Provenance 38)	0.924	0.3554
$\alpha_1$ (Provenance 39)	0.035	0.9717
$\alpha_1$ (Provenance 40)	0.303	0.7620
$\alpha_1$ (Provenance 43)	-1.146	0.2519
$\alpha_1$ (Provenance 44)	-0.886	0.3754
$\alpha_1$ (Provenance 51)	0.926	0.3542
$\alpha_1$ (Provenance 66)	1.759	0.0786
$\alpha_1$ (Provenance 67)	0.295	0.7676
$\alpha_1$ (Provenance 69)	1.316	0.1880
$\alpha_1$ (Provenance 70)	0.924	0.3553
$\alpha_1$ (Provenance 73)	0.481	0.6302
$\alpha_1$ (Provenance 77)	0.387	0.6985

$\alpha_1$ (Provenance 80)	-2.887	0.0038
$\alpha_1$ (Provenance 87)	-0.784	0.4329
$\alpha_1$ (Provenance 88)	0.608	0.5431
$\alpha_1$ (Provenance 90)	1.532	0.1256
$\alpha_1$ (Provenance 92)	-1.379	0.1680
$\alpha_1$ (Provenance 93)	0.670	0.5027
$\alpha_1$ (Provenance 94)	2.378	0.0174
$\alpha_1$ (Provenance 99)	1.566	0.1172

*Supplementary Table S6: Model-fitted coefficients for Spike knots below 0.5 m*

Parameter	Coefficient	p-value
$\alpha_0$ (Provenance 104)	-3.427	0.0006
$\alpha_1$ (Provenance 11)	-2.102	0.0355
$\alpha_1$ (Provenance 129)	-0.991	0.3218
$\alpha_1$ (Provenance 130)	-1.802	0.0714
$\alpha_1$ (Provenance 135)	-0.115	0.9082
$\alpha_1$ (Provenance 137)	-1.571	0.1162
$\alpha_1$ (Provenance 138)	-1.904	0.0569
$\alpha_1$ (Provenance 14)	-0.054	0.9570
$\alpha_1$ (Provenance 144)	-1.552	0.1207
$\alpha_1$ (Provenance 150)	0.509	0.6104
$\alpha_1$ (Provenance 161)	0.076	0.9393
$\alpha_1$ (Provenance 18)	0.154	0.8772
$\alpha_1$ (Provenance 26)	-0.128	0.8978
$\alpha_1$ (Provenance 28)	-0.319	0.7495
$\alpha_1$ (Provenance 36)	-2.071	0.0383
$\alpha_1$ (Provenance 37)	0.687	0.4920
$\alpha_1$ (Provenance 38)	-1.391	0.1641
$\alpha_1$ (Provenance 39)	-2.474	0.0133
$\alpha_1$ (Provenance 40)	-1.394	0.1632
$\alpha_1$ (Provenance 43)	-0.552	0.5809
$\alpha_1$ (Provenance 44)	-1.739	0.0820
$\alpha_1$ (Provenance 51)	2.369	0.0178
$\alpha_1$ (Provenance 66)	-1.123	0.2616
$\alpha_1$ (Provenance 67)	-0.593	0.5528
$\alpha_1$ (Provenance 69)	-0.586	0.5579
$\alpha_1$ (Provenance 70)	-0.152	0.8793
$\alpha_1$ (Provenance 73)	-2.299	0.0214
$\alpha_1$ (Provenance 77)	-1.092	0.2749
$\alpha_1$ (Provenance 80)	-1.162	0.2453

$\alpha_1$ (Provenance 87)	-1.368	0.1712
$\alpha_1$ (Provenance 88)	0.094	0.9247
$\alpha_1$ (Provenance 90)	-0.442	0.6584
$\alpha_1$ (Provenance 92)	-0.475	0.6344
$\alpha_1$ (Provenance 93)	-1.913	0.0557
$\alpha_1$ (Provenance 94)	-1.276	0.2021
$\alpha_1$ (Provenance 99)	-1.570	0.1163